SYSTEMATIC FOLIAR MORPHOLOGY OF PHYLLANTHOIDEAE (EUPHORBIACEAE). II. PHENETIC ANALYSIS[1]

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ABSTRACT

Leaf architectural and cuticular characters in the Phyllanthoideae (Euphorbiaceae) were analyzed using Similarity Graph Clustering. The resulting groups and their similarity relationships correspond remarkably well to classifications based on more traditional taxonomic characters. Exceptions generally appear to be either cases in which other evidence also suggests that previous classifications are invalid or in which total similarity could be expected to be a poor indicator of relationship. Obtaining such clear results in a group not known for having diagnostic leaf characteristics indicates the considerable potential foliar morphology has for classification of modern and fossil angiosperms.

This paper reports the first numerical analysis of leaf architectural and cuticular features of a related group of extant flowering plants. This is part of a project undertaken both to test the systematic potential of leaf characters at higher taxonomic levels and to explore the contribution of foliar morphology to the phylogeny of the Euphorbiaceae. Earlier studies (Dolph, 1976; Hill, 1980) have tested foliar character sets by attempting to correctly identify leaves taken from randomly selected, usually unrelated plants. For example, Hill collected five leaves each from 20 species of woody plants growing in a botanic garden. His sample included 19 genera from 12 families. Although both he and, to a lesser extent, Dolph achieved their stated goal of taximetrically grouping together leaves taken from the same species, neither was able to recognize any higher taxa using their methods and character sets.

I instead chose to test the systematic usefulness of a leaf character set in a natural group by comparing the results of numerical analysis of leaf characters with recent classifications based on more traditional sources of systematic data. I selected for study the Phyllanthoideae, putatively the most primitive subfamily of the Euphorbiaceae, because the long history of systematic interest in the family has resulted in a series of infrafamilial classifications based on characteristics drawn from a wide variety of organs (see reviews in Webster, 1967 and Hutchinson, 1969) and because of the broader phylogenetic significance of the subfamily in clarifying the rela-

tionships of the Euphorbiaceae. That the leaves of the Phyllanthoideae are relatively nondescript makes analysis of this group of additional interest. The recent treatment by Webster (1975; see Table 1), who integrated evidence from floral morphology, palynology, cytology, and wood anatomy, serves as the principal classification with which to compare the foliar analysis.

I derived leaf architectural characters from the system proposed by Hickey (1973). Although the use of this character set for numerical analysis has been criticized because many characters do not have equidistant quantitative states (Hill, 1980), the characters have been shown to be of systematic importance at higher taxonomic levels (Hickey & Wolfe, 1975). Cuticular characters were selected from the list prepared by Stace (1965; see also Dilcher, 1974). In another paper (Levin, 1985), I discussed the characters and their states and described the leaves of the 51 genera in the Phyllanthoideae that I examined. In a future paper (Levin, in press), I will present the results of a cladistic analysis of the same data set.

MATERIALS AND METHODS

DATA GATHERING PROCEDURES

The taxa included in this study are listed in Table 1, along with the numbers I assigned to them for convenience of representation in Figures 1–6. For reasons that I explain below, I have deleted from the list all the taxa with phyllan-

TABLE 1. Taxa includes in study and numbers assigned to OTUs. Classification follows Webster (1975).

Number	Taxon
WIELANDIEAE	
1	*Wielandia*
2	*Astrocasia*
9	*Blotia*
5	*Discocarpus*
3	*Heywoodia*
4	*Lachnostylis*
13	*Pentabrachium*
8	*Petalodiscus*
6	*Savia* sect. *Heterosavia*
7	*S.* sect. *Savia*
AMANOEAE	
10	*Amanoa*
11	*Actephila* group 1: *A. anthelminthica, A. nitida*
12	*A.* group 2: *A. excelsa*
93	*Croizatia*
BRIDELIEAE	
14	*Bridelia* group 1: sects. *Micrantheae* pro parte, *Scleroneurae* pro parte
15	*B.* group 2: sect. *Cleistanthoideae*
	B. group 3: sects. *Micranthae* pro parte, *Scleroneurae* pro parte, *Stipulares*
17	*Cleistanthus acuminatissimus*
18	*C.* sect. *Stipulati*
19	*C.* sects. *Ferruginosi, Pedicellati*
20	*Cleistanthus* sect. *Chartacei*
21	*C.* sect. *Cleistanthus*
22	*C. saichikii*
23	*C.* sect. *Australes*
24	*C.* sect. *Leiopyxis*
DICOELIEAE	
25	*Dicoelia*
PORANTHEREAE	
26	*Andrachne* sects. *Arachne, Phyllanthidia*
27	*A.* sect. *Phyllanthopsis*
SPONDIANTHEAE	
28	*Spondianthus*
ANTIDESMEAE	
29	*Antidesma* sects. *Roxburghiana, Venosa* pro parte
30	*A.* sects. *Laciniata, Venosa* pro parte
31	*A.* sect. *Tetrandra*
32	*A.* sect. *Montana*
33	*A.* sect. *Velutinosa*
34	*A.* sect. *Ghaesembilla*
35	*Celianella*
36	*Hyeronima*
37	*Leptonema*
38	*Thecacoris*

TABLE 1. Continued.

Number	Taxon
APORUSEAE	
39	*Aporusa*
40	*Ashtonia*
41	*Baccaurea* sects. *Everettiodendron, Calyptroon*
42	*B.* sect. *Pierardia*
43	*B. Dubiae*
44	*B.* sect. *Isoandrion*
45	*Didymocistus*
46	*Maesobotrya*
47	*Protomegabaria*
48	*Richeria*
DRYPETEAE	
49	*Drypetes* sects. *Drypetes* pro parte, *Sphragidia* pro parte
50	*D.* sects. *Drypetes* pro parte, *Sphragidia* pro parte
51	*D.* sect. *Sphragidia* pro parte
52	*D.* sects. *Oligandrae* pro parte, *Stemonodiscus, Stenogynium, Stipulares* pro parte
53	*D.* sects. *Oligandrae* pro parte, *Stipulares* pro parte
54	*D.* sect. *Drypetes* pro parte
90	*Neowawraea*
55	*Putranjiva*
PHYLLANTHEAE	
Securineginae	
56	*Jablonskia*
57	*Keayodendron*
58	*Meineckia*
59	*Pseudolachnostylis*
60	*Zimmermannia*
Flueggeinae	
61	*Flueggea*
67	*Margaritaria*
UAPACEAE	
88	*Uapaca*
HYMENOCARDIEAE	
89	*Hymenocardia*
BISCHOFIEAE	
91	*Bischofia*
INCERTAE SEDIS	
92	*Martretia*

thoid branching, in which plagiotropic branch systems resemble pinnately compound leaves (OTUs 62–66 and 68–87). In all but a few cases, I studied cleared leaves of a minimum of 10% of the species of each genus. I then grouped the

TABLE 2.   Characters and character states. See Hickey (1973), Dilcher (1974), and Levin (1985) for more explanation. The type of each character, and for ordered characters the value chosen for j, is indicated in parentheses.

1. Organization: Simple or Compound. (Simple)
2. Base Balance: Symmetrical or Asymmetrical. (Simple)
3. Margin: Entire, Entire or crenate, but with glands, or Toothed. (Ordered, 1)
4. Venation: Brochidodromous, Weakly brochidodromous, or Eucamptodromous. (Ordered, 1)
5. Primary size: Moderate, Stout, or Massive. (Ordered, 1)
6. Secondary angle: Narrow (<45°), Moderate, or Wide (>65°). (Ordered, 1)
7. Angle of basal secondaries, relative to adjacent secondaries: More acute, Similar, or More obtuse. (Ordered, 1)
8. Angle of lower secondaries, relative to middle secondaries: More acute, Similar, or More obtuse. (Ordered, 1)
9. Angle of upper secondaries, relative to middle secondaries: More acute, Similar, or More obtuse. (Ordered, 1)
10. Secondary course: Curved uniformly or Curved abruptly. (Simple)
11. Angle of secondary loops: Acute, Right, or Obtuse. (Ordered, 1)
12. Size of outer loops: Irregular, Uniform, Decreasing upwards, or Absent. (Ordered, 1)
13. Tertiary angle of origin, admedial: Acute, Right, or Obtuse. (Ordered, 1)
14. Teritary angle of origin, exmedial: Acute, Right, or Obtuse. (Ordered, 1)
15. Tertiary pattern: Ramified, Random reticulate, Orthogonal reticulate, Weakly percurrent, Strongly percurrent with angle to midrib oblique, or Strongly percurrent with angle to midrib predominantly right. (Ordered, 3)
16. Simple intersecondaries: Absent or Present. (Simple)
17. Composite intersecondaries: Absent, Infrequent (in fewer than 20% of intercostal areas), or Frequent (in more than 20% of intercostal areas). (Ordered, 1)
18. Intramarginal vein: Absent or Present. (Simple)
19. Higher order vein pattern: Ramified, All random, 4° orthogonal and higher orders random, or 4° and 5° orthogonal. (Ordered, 2)
20. Higher order vein size: 4° moderate and 5° heavy, All moderate, 4° moderate and 5° fine, or 4° and 5° fine. (Ordered, 2)
21. Highest order present: 4°, 5°, or 6°. (Ordered, 1)
22. Areole development: Incomplete, Imperfect, or Well-developed. (Ordered, 1)
23. Areole arrangement: Random or Ordered. (Simple)

TABLE 2.   Continued.

24. Areole shape: Irregular or Regular. (Simple)
25. Areole size: Large, Medium, or Small. (Ordered, 1)
26. Veinlets: Absent, Simple, Branched 1–2×, or Branched 2–3×. (Ordered, 2)
27. Prismatic crystals in mesophyll: Absent or Present. (Simple)
28. Prismatic crystals with veins: Absent or Present. (Simple)
29. Druses in mesophyll: Absent or Present. (Simple)
30. Druses with veins: Absent or Present. (Simple)
31. Epidermal anticlinal walls, adaxial: Straight or Undulate. (Simple)
32. Epidermal anticlinal walls, abaxial: Straight or Undulate. (Simple)
33. Epidermal papillae: Absent or Present. (Simple)
34. Stomatal location: Abaxial only, Primarily abaxial but a few adaxial, or Approximately equal on both surfaces. (Ordered, 1)
35. Stomatal index (abaxial): <10%, 10–20%, or >20%. (Ordered, 1)
36. Stomatal type: Paracytic or Anisocytic. (Simple)
37. Water stomata: Absent or Present. (Simple)
38. Unicellular trichomes: Absent, Solitary, or Some tufted. (Ordered, 1)
39. Uniseriate, multicellular trichomes: Absent or Present. (Simple)
40. Peltate trichomes: Absent or Present. (Simple)
41. Filiform sclereids in mesophyll: Absent or Present. (Simple)
42. Tanniniferous epidermal cells: Absent or Present. (Simple)
43. Sclerified epidermal cells: Absent or Present. (Simple)

species into homogeneous groups, which generally correspond to sections or undivided genera. I treated each group as an operational taxonomic unit, or OTU, for this study. Details of the procedures I used for collecting and clearing the leaves and for selecting the OTUs have been published in another paper (Levin, 1986).

Table 2 lists the 43 characters I scored for each leaf. These characters and their states are described by Stace (1965), Hickey (1973), and Levin (1986). All are binary or multistate qualitative characters. The basic data matrix has been published elsewhere (Levin, 1986: table 1) and will not be reproduced here.

DATA-ANALYTIC METHOD

Rather than using a clustering method like UPGMA that merely indicates the level of similarity at which a taxon or group of taxa first joins

another taxon or group of taxa and expresses the results in the form of a dendrogram, I chose to use Similarity-Graph Clustering (SIMGRA). This method, because it does not force the results into a hierarchical form but instead shows all relationships at a given similarity level, summarizes the reticulate structure of the similarity matrix far more completely than do other clustering methods (Prance et al., 1969; Legendre & Rogers, 1972). The theoretical and mathematical frameworks of SIMGRA can be found in Estabrook (1966), Estabrook and Rogers (1966), Wirth et al. (1966), and Legendre and Rogers (1972), and other examples of its use in Prance et al. (1969), Rogers and Fleming (1973), and Duncan (1980). The explanation presented here is derived from these references.

The SIMGRA algorithm consists of two steps. First, a similarity measure is calculated for all pairs of objects (the OTUs in Table 1). The similarity measure used here is the generalized Simple Matching Coefficient of Estabrook and Rogers (1966). This is defined as:

$$S(a,b) = \frac{\sum\limits_{k=1}^{n} S_k(a,b)}{n}$$

where $S(a,b)$ is the similarity between any two OTUs a and b, $S_k(a,b)$ is the partial similarity between a and b for any character k, and n is the number of characters used to compare the OTUs. If OTUs a and b share the same state for character k, then $S_k(a,b) = 1$. If the two OTUs differ for character k, then one of three rules may be chosen by the taxonomist to calculate $S_k(a,b)$:

1. $S_k(a,b) = 0$ (simple character);

2. $S_k(a,b) = \dfrac{2(j + 1 - d)}{2j + 2 + dj}$ whenever $d \le j$

   $= 0$ when $d > j$,

   where j is the maximum number of character states by which two OTUs may be separated and still be considered at all similar, and d is the distance apart that the two states are in a pre-specified ordering of the states (ordered character); or

3. $S_k(a,b) =$ arbitrary values assigned by the taxonomist in advance, by providng a matrix of values between 0 and 1 (matrix character).

Thus the partial similarities for both ordered and matrix characters involve subjective decisions on the part of the taxonomist. For the ordered characters in this study, I set the value of j for character k at the number of character states for that character less two or three; these values cause only the most extreme distances between character states to yield a partial similarity of 0. There were no matrix characters in this study. The type of each character and, for ordered characters, the value of j, are indicated in Table 2.

After an overall similarity value $S(a,b)$ has been calculated for each pair of OTUs, the similarity values are examined in order of decreasing magnitude. At each level of similarity, a connection is formed between two OTUs if they are at least as similar as the specified level. A cluster is a group of OTUs for which there exists at least one continuous pathway of connections joining the OTUs. The procedure continues until all the OTUs belong to one cluster. In this study, I used the program SIMGRA by G. F. Estabrook (Univ. of Michigan) on an IBM 4341 at the University of California at Berkeley.

RESULTS

During the SIMGRA analysis, clusters were formed and enlarged at 45 levels of similarity. I grouped these levels and summarized them in Figures 1–6. On each drawing the lowest similarity value at which connections were made (S), the levels summarized (L), and the number of OTUs that have not yet formed a connection with any other OTU (single member clusters or SMCs) are listed on the left side. Each OTU that has formed a connection with another is indicated by a number, as listed in Table 1. Connections formed at any of the similarity levels summarized are represented by dashed lines, connections formed at previous levels by solid lines. In the following discussion, clusters are referred to by the prefix "C-," followed by the lowest-numbered OTU belonging to the cluster. Within a cluster, tightly connected subsets of OTUs that are less tightly connected to other subsets are termed subclusters and referred to by the prefix "SC-," with the lowest-numbered OTU as the suffix. For highly connected groups, either clusters or subclusters, it is often inconvenient to show all the connections. Such a group of OTUs, therefore, is shown diagrammatically as a circle, with the OTUs forming the cluster representing by placing their numbers at the edge of the circle. The fraction in the center, in which the numerator equals the number of connections actually formed within the cluster and the de-
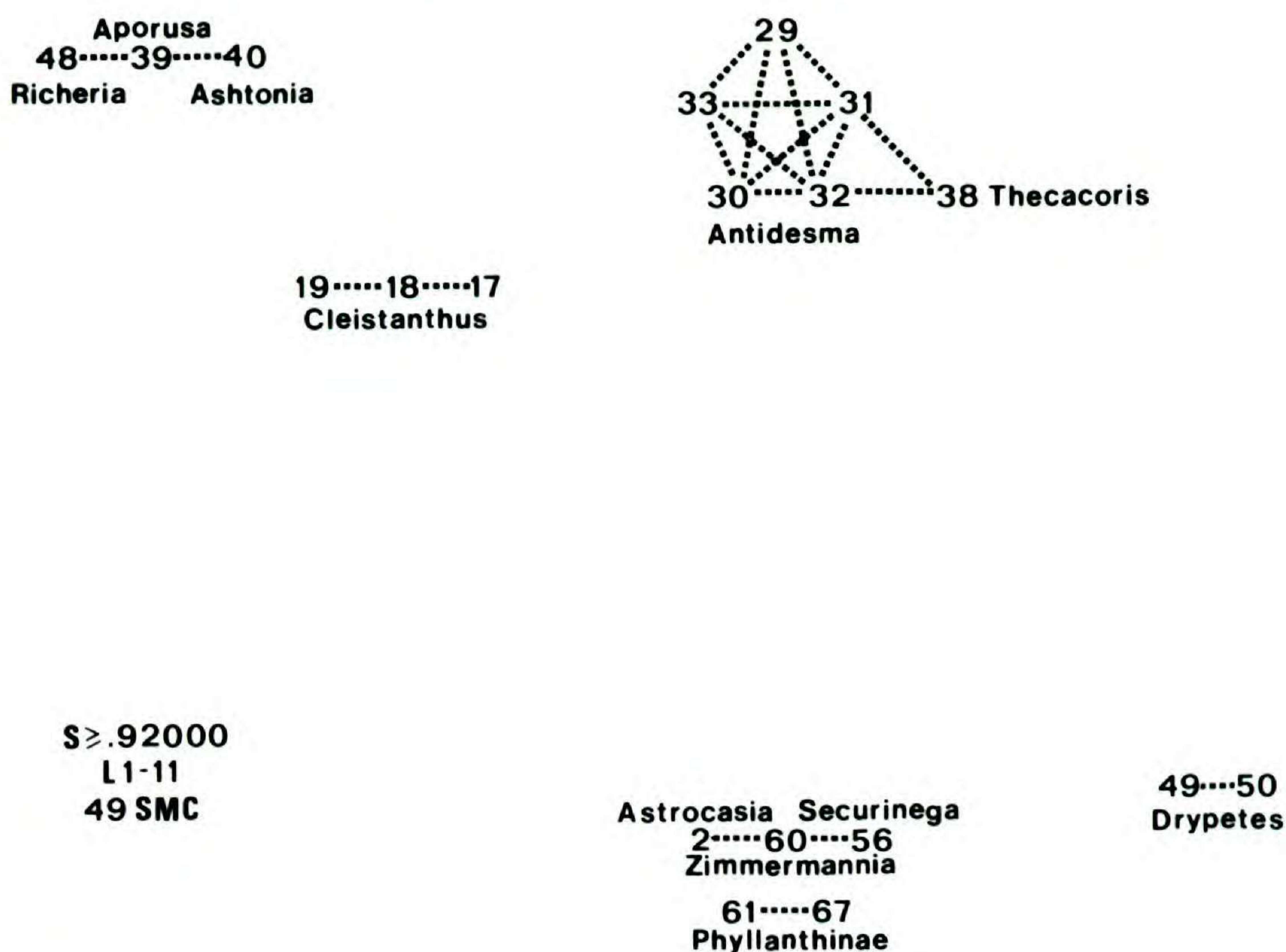
FIGURE 1. Clusters present in SIMGRA analysis at level II or similarity value 0.92000. In this and all following figures, OTUs are represented by numbers, as listed in Table 1. Dashed lines indicate connections formed between OTUs at any of the similarity levels summarized in the figure, thin solid lines indicate connections formed at previous levels, and thick solid lines indicate connections between circular subclusters. The lengths of lines reflect the constraints of two-dimensional representation and in no way indicate the degree of connectedness between the groups. See text for further explanation.

nominator equals the number of connections that are possible, indicates the connectedness of the cluster's members. Connections between circular subclusters, designated by the prefix "CSC-," are represented by a heavy solid line accompanied by a fraction that represents the degree of connectedness between the subclusters; again, the numerator of the fraction indicates the number of actual connections and the denominator equals the number of possible connections between the OTUs in the two subclusters. The length of the line bears no relationship to the connectedness between the groups.

Initially, I included all the OTUs for which I had data (Levin, 1985: table 1) except for *Lingelsheimia*, which I received after I had completed all the SIMGRA analysis. It immediately became clear that members of the Flueggeineae exhibited overwhelming convergence with other OTUs, completely obscuring relationships both within the subtribe and between the other OTUs. The foliar morphology of this species-rich group has apparently undergone an adaptive radiation, associated with the evolution of phyllanthoid branching, in which determinate lateral branchlets mimic pinnately compound leaves (Webster, 1956, 1967; Levin, 1985). Fortunately for the

systematist, the more primitive members of the subtribe, *Flueggea*, *Margaritaria*, *Richeriella*, and a few species of *Phyllanthus*, retain the normal habit. I therefore removed the genera with phyllanthoid branching (*Breynia*, *Glochidion*, *Phyllanthus*, *Sauropus*, and *Synostemon*) from the analysis, leaving the 68 OTUs in Table 1.

After the first 11 similarity levels (Fig. 1), 19 OTUs have joined to form six clusters, and 49 OTUs remain as SMCs. The only large cluster, C-29, consists of *Thecacoris* (OTU 38) and a completely interconnected subcluster containing all but one section of *Antidesma*. The other clusters have only two or three members and are minimally connected. As Figure 1 indicates, the first-formed clusters generally consist of OTUs from a single genus or of closely related genera, which might be expected to be quite similar. Had *Lingelsheimia* been included in the analysis, it would have joined C-2 through a connection with *Zimmermannia* (60) at level 6.

The next seven levels, to S = 0.90000 (Fig. 2), see the formation of five new two-membered clusters and the enlargement of the earlier-formed clusters. Two new internal connections form in C-29, very tightly connecting *Thecacoris* to the other OTUs in the cluster. C-2 and C-61 join to
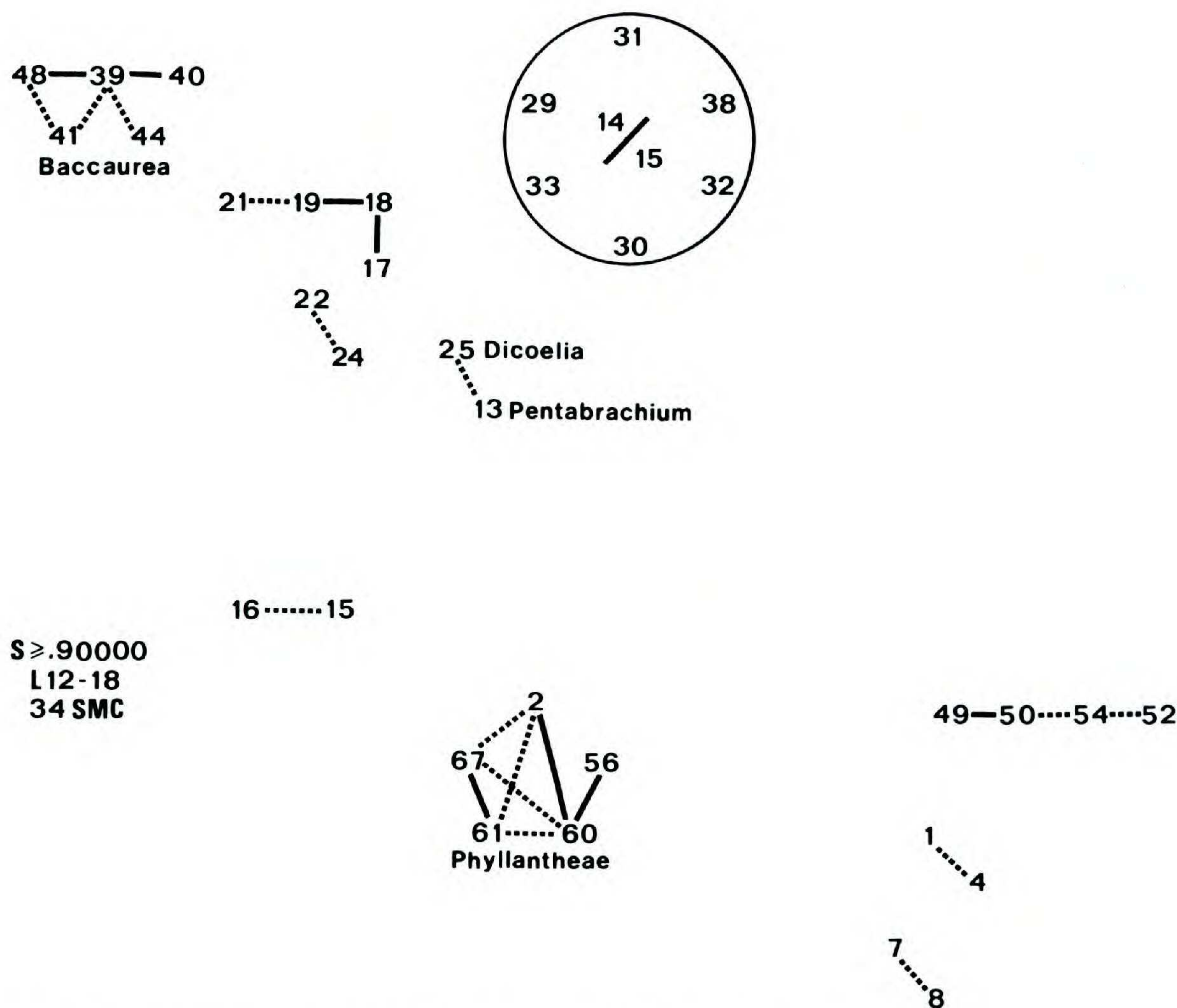
FIGURE 2.   Clusters present in SIMGRA analysis at level 18 or similarity value 0.90000.

form a single cluster, with OTU 56, *Jablonskia*, connected to only one OTU of an otherwise completely interconnected cluster of members of the Phyllantheae. The clusters representing *Cleistanthus* and *Drypetes* each gain one or two new OTUs belonging to their respective genera, but each cluster remains minimally interconnected. Two sections of *Baccaurea* rather loosely join C-39. Thirty-four SMCs remain.

By similarity level 0.88222 (Fig. 3), only one new cluster forms and C-1 remains unchanged. The most marked change is the joining of C-13, C-17, C-22, and C-29 into a single cluster. CSC-29 is joined by other OTUs in the Antidesmeae, *Antidesma* sect. *Ghaesembilla* (34) and *Hyeronima* (36). C-2, C-49, and C-39 become more tightly connected internally, and the latter is joined by OTU 46, *Maesobotrya*. OTUs 6 and 9 connect to C-7, which now consists of *Savia* and its segregates *Blotia* and *Petalodiscus*. OTU 14 joins the other OTUs in *Bridelia*. Twenty-five SMCs remain.

By level 31 (Fig. 4), only 16 SMCs remain. C-1 and C-6 join by a connection between *Wielandia* (1) and *Savia* (6) to form most of the Wielan-

dieae. No new internal connections form within C-2, but it is joined by three genera, *Heywoodia* (3), *Keayodendron* (57), and *Bischofia* (91). C-39 joins CSC-29 by a single connection between OTUs 36 and 40, and also forms connections with a section of *Baccaurea* (43), *Protomegabaria* (47), and *Uapaca* (88). In other portions of C-13, additional connections form between the subclusters, with two sections of *Cleistanthus* (22 and 24) beginning to become connected to the other sections of the genus. A connection between OTUs 11 and 12 joins the two OTUs in *Actephila*; the latter OTU had earlier connected with a section of *Andrachne* (27). *Neowawraea* (90) joins *Bridelia* (C-14), and *Putranjiva* (55) forms a single connection with its close relative *Drypetes* (C-49), whose members are becoming increasingly tightly interconnected.

Levels 32 through 37 (Fig. 5) see connections forming to seven SMCs and the coalescence of the earlier clusters into two large clusters. Connections between OTUs 1 and 55, 6 and 56, and 55 and 56 loosely join CSC-1 (Wielandieae pro parte), CSC-2 (roughly the Phyllantheae), and CSC-49 (Drypeteae). These subclusters remain
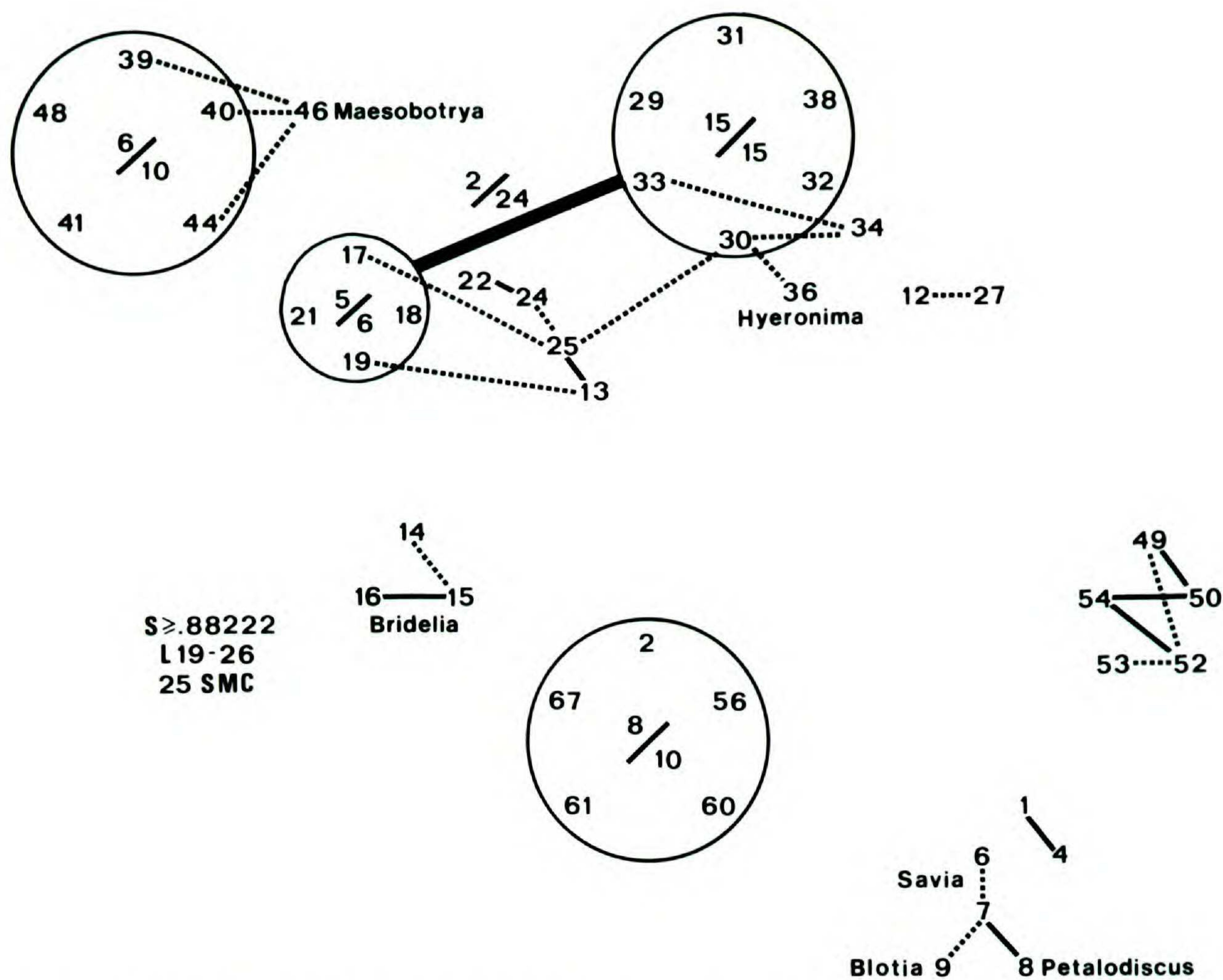
FIGURE 3.   Clusters present in SIMGRA analysis at level 26 or similarity value 0.88222.

relatively unchanged at these levels: CSC-1 gains two internal connections, CSC-2 gains OTU 20, a section of *Cleistanthus*, by a connection with OTU 60, and CSC-49 gains one internal connection and another group in *Drypetes*, OTU 51. OTUs 27 and 38 connect to 26, thereby joining CSC-11 to CSC-29, the core genera of the Antidesmeae. No new connections form between CSC-13 and CSC-29, and only one between CSC-13 and CSC-17. CSC-17 gains SC-22, thus further consolidating *Cleistanthus*, and *Meineckia* (58) connects to OTU 24. *Hymenocardia* (89) simultaneously joins both *Neowawraea* (90) and OTU 18 to connect SC-14 to CSC-17. CSC-29, in addition to becoming increasingly highly internally connected, increases its association with CSC-17 through four new connections and with CSC-39 through three. CSC-39 gains only OTU 42, but increases both its internal connectedness and its connectedness to OTU 47. This subcluster now corresponds to the Aporuseae of Webster (1975), less *Didymocistus* (45), which remains among the nine SMCs.

At level 45 (Fig. 6), all OTUs belong to one cluster. This large cluster is composed of eight circular subclusters and six fairly isolated OTUs. The Wielandieae pro parte, CSC-1, in addition to becoming more tightly connected internally, gain *Discocarpus* (5) through a connection to *Petalodiscus* (8), form a new connection to CSC-11, and connect further to CSC-2 both directly and through newly added OTUs 10 (*Amanoa*) and 93 (*Croizatia*). The connection between CSC-1 and CSC-2 is the strongest between any two subclusters. CSC-2, which with the addition of *Pseudolachnostylis* (59) consists of most of the Phyllantheae, *Astrocasia* (2) and *Heywoodia* (3) of the Wielandieae, and a section of *Cleistanthus*, connects with six other subclusters, albeit generally weakly. *Amanoa* (10), *Celianella* (35), and *Croizatia* (93) all form connections with CSC-2 late in SIMGRA analysis; in fact *Amanoa* is the last OTU to join the cluster, connecting simultaneously to OTUs 1 and 56 at level 45. CSC-11 (*Actephila* and *Andrachne*), CSC-14 (*Bridelia*), and CSC-45 (*Didymocistus*, *Hymenocardia*, and *Neowawraea*) become very highly or completely internally connected subclusters that remain fair-

FIGURE 4.   Clusters present in SIMGRA analysis at level 31 or similarity value 0.87111.

ly isolated from other subclusters. CSC-49, the Drypeteae less *Neowawraea,* is less tightly internally connected than these, but also is quite isolated. Two OTUs connect to CSC-11: a section of *Cleistanthus* (23), which connects at level 38, and *Martretia* (92), which connects at level 42. *Leptonema* (37) forms six connections to members of SC-29, which, together with CSC-17, simultaneously joins to CSC-13. CSC-13 thus consists of most of *Cleistanthus* (17–19, 21, 22, and 24), *Dicoelia* (25), *Meineckia* (58), *Pentabrachium* (13), and the Antidesmeae (29–34, 36–38) less *Celianella* (35). *Spondianthus* (28) forms six connections to SC-29. The final subcluster, CSC-39, consisting of the relatively tightly connected Aporuseae (39–44, 46–48) more loosely joined by *Uapaca* (88), connects fairly closely with CSC-13, but is otherwise comparatively isolated.

In addition to the SIMGRA analysis using both architectural and cuticular characters, I also performed an analysis using only the 26 architectural characters in order to examine their power to group the OTUs. The results were similar in both cases. Inclusion of the genera with phyllanthoid branching introduced convergence that muddled the clusters, so I again deleted them. The same major clusters formed in approximately the same order, but tended to be somewhat less tightly connected internally and to have more connections to other clusters. This was particularly true of CSC-2, which consists of genera Webster (1975) placed in the Phyllantheae and the Wielandieae. CSC-39, the Aporuseae and Uapaceae, appeared more similar to the Antidesmeae when only architectural characters rather than all the foliar characters were used. *Cleistanthus,* with *Dicoelia* and *Pentabrachium,* remained more distinct from the Antidesmeae, so that at the conclusion of the clustering, CSC-13 of Figure 6 would have been represented better by two circular subclusters. Thus the inclusion of cuticular characters generally improved the resolution of the groups but may have caused a few to appear more similar than they otherwise
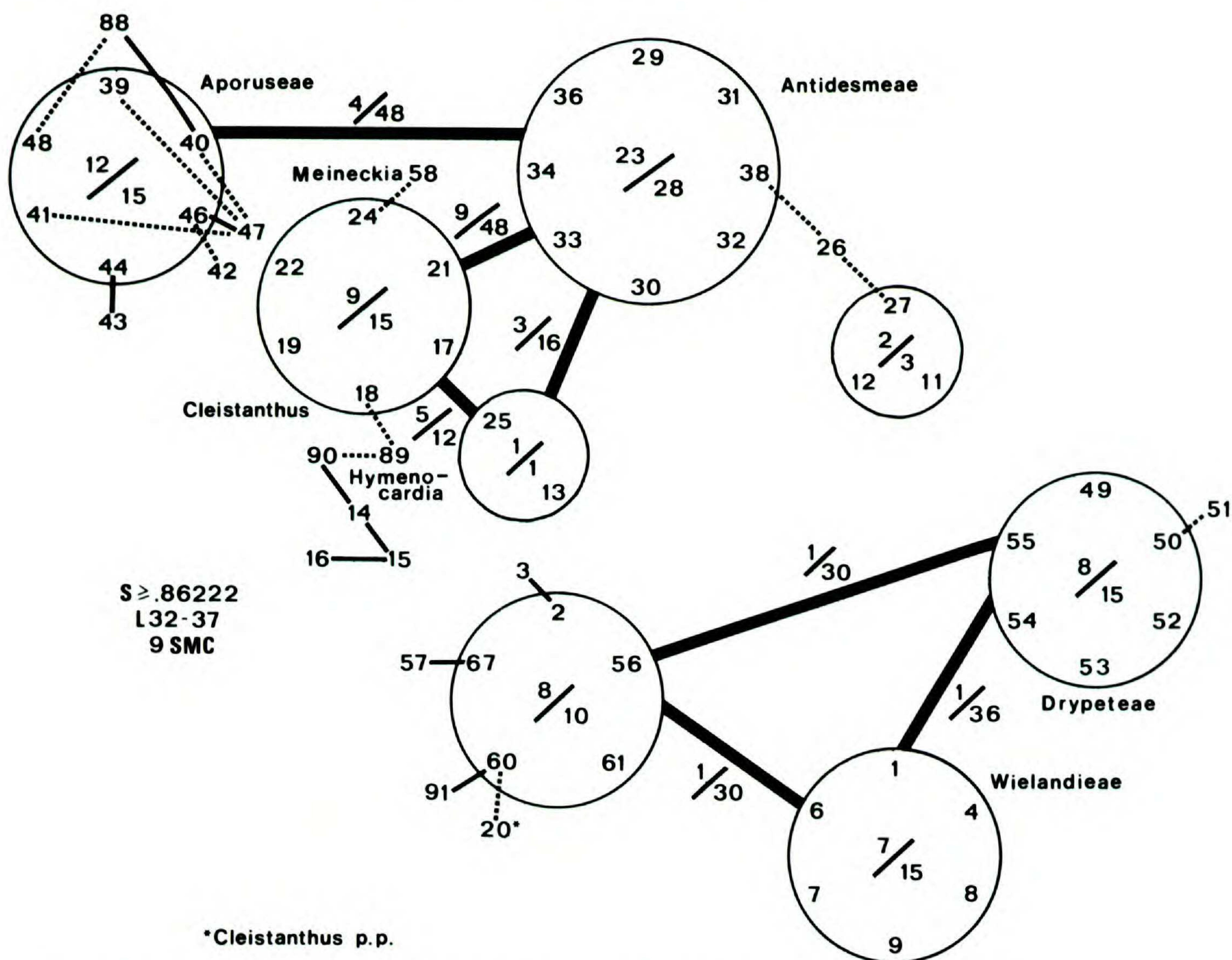
FIGURE 5. Clusters present in SIMGRA analysis at level 37 or similarity value 0.86222.

might. I attempted no analysis using only cuticular characters because too few characters were involved.

DISCUSSION

COMPARISON WITH PREVIOUS CLASSIFICATIONS

The groups that formed during SIMGRA analysis of leaf characters alone correspond remarkably well to taxa proposed by other systematists, particularly Webster (1975), whose use of different sources of systematic information was the most comprehensive. The large subclusters in Figures 5 and 6 are almost equivalent to his major tribes, notably the Antidesmeae, Aporuseae, Drypeteae, Phyllantheae, and Wielandieae. Several genera he and others have considered very isolated based on other characters, e.g., *Bischofia, Hymenocardia, Martretia,* and *Spondianthus,* connect late in the analysis, corroborating their distinctiveness. Furthermore, putative relationships between taxa are frequently reflected

by the degree of connectedness between the corresponding subclusters, as in the cases of the comparatively close associations between the Antidesmeae and the Aporuseae, *Spondianthus* and the Antidesmeae, and between the Phyllantheae and the Wielandieae, and the relatively isolated position of the Drypeteae.

A one-to-one correspondence does not exist between the SIMGRA results and any previous classification, however, and there are several notable discrepancies. One of the most obvious of these involves the genus *Cleistanthus,* which I divided into eight OTUs that approximate sections (OTUs 17–24). Of these, four became very highly connected by level 31 (Fig. 4; CSC-17), and two more joined the subcluster soon thereafter (Fig. 5). The two remaining OTUs, sects. *Chartacei* (20) and *Australes* (23), remained SMCs until late in the analysis, and even then did not form connections with the *Cleistanthus* subcluster. *Chartacei* formed connections with eight OTUs, five of which are in CSC-2 and none of
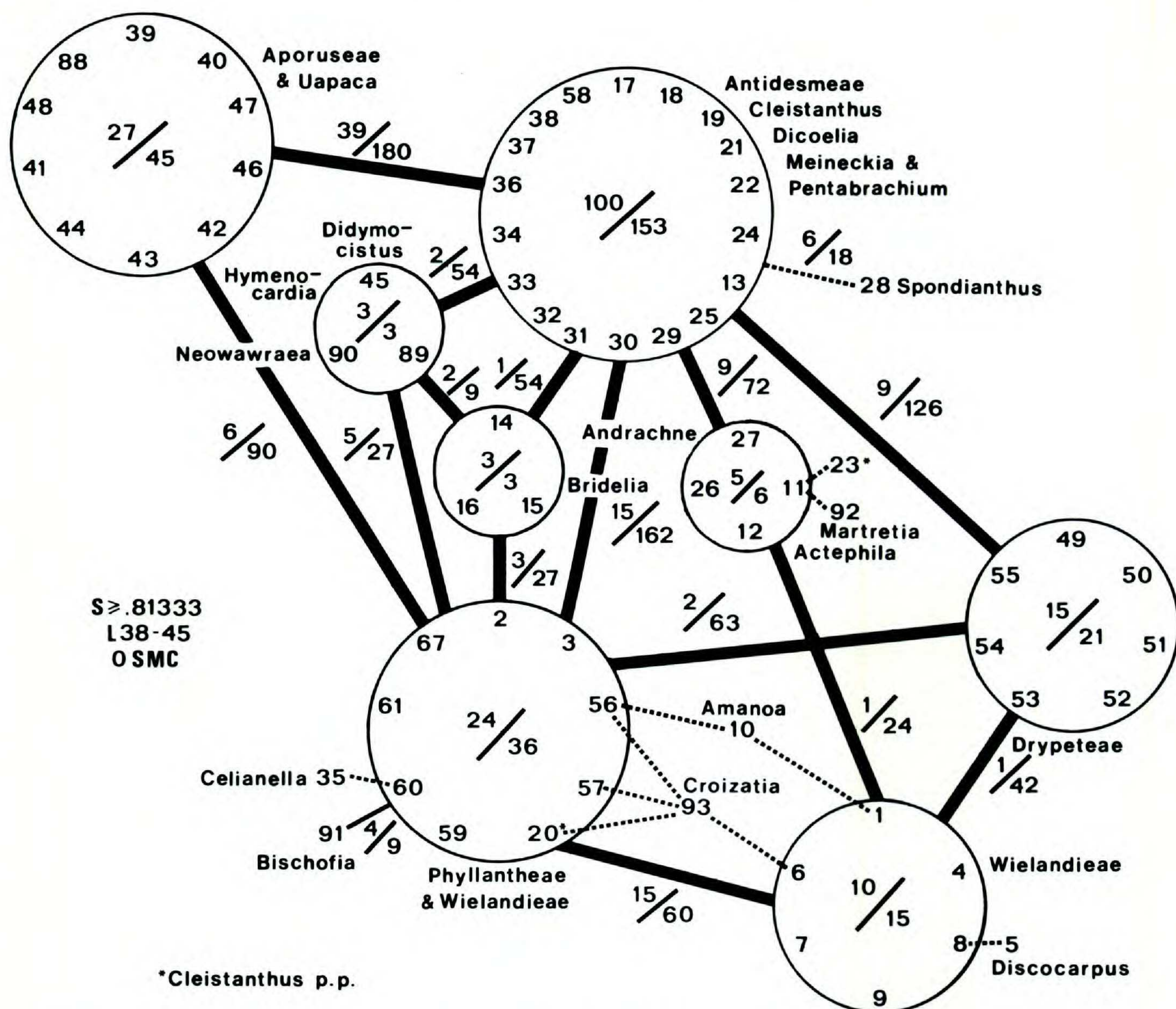
FIGURE 6.   Clusters present in SIMGRA analysis at level 45 or similarity value 0.81333.

which are in *Cleistanthus. Australes* are even more distant, forming a single connection to *Actephila* at level 38. Jablonsky (1915) felt that *Australes*, although clearly in *Cleistanthus*, are rather isolated within the genus and also noted that the leaves of *C. cunninghamii*, the only species in *Chartacei* I examined, are not typical of the section. Apparently leaves of these two taxa exhibit sufficient non-divergent change that overall similarity poorly reflects relationship.

In most systems *Cleistanthus* and *Bridelia* (14–16) are considered to be closely related because they have very similar flowers with valvate sepals (Jablonsky, 1915) and similar pollen (Punt, 1962; Köhler, 1965). Webster (1975), on the basis of the pollen evidence, placed the two genera in their own tribe near the Wielandieae. Phenetic analysis of the foliar characters considerably separates the two genera. Most members of *Cleistanthus* were closely allied with *Dicoelia* and the

Antidesmeae, whereas *Bridelia* remained fairly isolated and formed only a single connection with *Cleistanthus* at the final level of similarity. *Bridelia* leaves are extremely specialized within the Phyllanthoideae (Levin, 1986), and therefore appear isolated in a phenetic analysis. Cladistic analysis, which de-emphasizes the unique character states (autapomorphies) of *Bridelia*, supports the relationship between the genera (Levin, in press).

Another difference from the classifications of Webster and others lies in the assignment of genera to the Wielandieae and the Phyllantheae. In particular, leaves of *Astrocasia* (2) and *Heywoodia* (3), genera usually included in the Wielandieae, are more similar to leaves of the Phyllantheae. Webster (1956) had previously suggested a relationship between *Astrocasia* and the Phyllantheae, and both Punt (1962) and Köhler (1965) remarked on the close resemblance

among the pollen of these taxa. Pollen and other reproductive structures of *Heywoodia* are less similar to the Phyllantheae. The main reason for retaining *Astrocasia* and, to a lesser extent, *Heywoodia* in the Wielandieae is their petaliferous flowers, a characteristic that, because it is primitive in the subfamily (Webster, 1967), might not necessarily be expected to reflect phylogenetic relationships. Cladistic analysis of the foliar characters in fact clearly associates *Astrocasia* with the Phyllantheae but retains *Heywoodia* in the Wielandieae (Levin, in press).

Meineckia (58), placed in the Phyllantheae by Webster (1965, 1975), connected with the bulk of *Cleistanthus* late in the SIMGRA analysis (Figs. 5, 6). Associated with the herbaceous tendencies of *Meineckia* is a reduction in the organization of its leaves (Levin, 1986), which obscures its relationships. A similar phenomenon probably explains the unexpected connection at level 43 between *Celianella* (35), a member of the Antidesmeae (Jablonsky, 1965; Webster, 1975), and *Zimmermannia* (60) of the Phyllantheae (Fig. 6). The leaves of *Celianella* are quite thick and have unusual reduced venation (Levin, 1986). In both of these cases, cladistic analysis of leaf characters yields results that are much closer to the classifications of Webster (1975) and others (Levin, in press).

Another difference between the SIMGRA results and Webster's (1975) classification involves the treatment of *Amanoa* (10), *Actephila* (11,12), and *Croizatia* (93), which Webster included in their own tribe, the Amanoeae. At similarity level 45, the final level shown in the SIMGRA analysis (Fig. 6), *Amanoa* simultaneously formed connections with *Wielandia* (1) and *Jablonskia* (56), and at only slightly lower similarity levels additional connections would form between *Amanoa* and other OTUs in CSC-1, containing genera in the Wielandieae, but not with either *Actephila* or *Croizatia*. Thus *Amanoa* appears most closely related to the Wielandieae, a relationship also suggested by pollen morphology (Punt, 1962; Köhler, 1965).

The leaves of *Actephila* (11, 12), in contrast, more closely resemble those of *Andrachne* (26, 27). The two genera first connected at level 24 (Fig. 3), and, by the end of SIMGRA analysis, they formed a tightly connected and rather isolated subcluster (Fig. 6). Both Punt (1962) and Köhler (1965) emphasized the similarity between the pollen of *Andrachne* and *Actephila*. Again, although SIMGRA analysis of the foliar morphology contradicts previous classifications, the concordance with pollen implies that leaf results may better reflect actual relationships.

Croizatia (93) has similar fruits to *Actephila* (Steyermark, 1952) but has very different leaves (cf. Fig. 6). Until *Croizatia* is better known, its relationships will remain uncertain.

In addition to its implications regarding the relationships of *Actephila,* the constitution of CSC-11 is significant also in that *Andrachne* sect. *Phyllanthopsis* (27) has been placed in *Savia* (6 and 7; CSC-1) by many authors (e.g., Pax & Hoffman, 1922), although palynology (Punt, 1962; Köhler, 1965) and some aspects of floral morphology (Webster, 1967) suggest that this section is in fact better placed in *Andrachne,* in accord with the leaves. The most striking feature uniting the leaves of different *Andrachne* sections is their anisocytic stomata, which is a derived condition in the Phyllanthoideae (Levin, in press).

Previously unsuspected on other evidence is the relationship suggested by foliar morphology between *Uapaca* (88) and the Aporuseae (CSC-39, Fig. 6). As I discussed previously (Levin, 1985), floral morphology, palynology, and wood anatomy, which have been the principal sources of taxonomic information in the Phyllanthoideae, have little to offer toward clarifying the relationships of *Uapaca* because it has so many unique specializations. However, in SIMGRA analysis, as in cladistic analysis (Levin, in press), both the totality of foliar characters and architectural characters alone consistently associate *Uapaca* with the Aporuseae. These foliar results suggest that the other organs of the genus be reexamined with this possible relationship in mind.

Equally novel is the suggestion (Fig. 6, CSC-45) of relationships between *Didymocistus* (45), *Hymenocardia* (89), and *Neowawraea* (90). Webster (1975), following other authors, placed these genera in three different tribes: the Aporuseae, the monotypic Hymenocardieae, and the Drypeteae, respectively. Both *Didymocistus* and *Neowawraea* have leaves that would be quite anomalous in the tribes to which Webster referred them (Levin, 1986). The high degree of organization of the venation makes all three genera quite similar to each other and to the Phyllantheae, as does wood anatomy (Metcalfe & Chalk, 1950; Hayden & Brandt, 1984; Mennega, 1984). The palynological literature has little to offer, because *Hymenocardia* has very unique pollen and the other two genera have not been examined.

Finally, Webster (1975) excluded *Martretia* (92) from the Phyllanthoideae, and indeed from the Euphorbiaceae altogether, although previous authors had placed it in the Antidesmeae. Its fruit and pollen characters are indeed unique in the family (Levin, 1986), and because it is one of the last OTUs to join a cluster in SIMGRA analysis, Webster may have been correct to remove *Martretia* from the Phyllanthoideae, if not also from the family.

POTENTIAL FOR USE IN IDENTIFICATION

Both Dolph (1976) and Hill (1980) had as their primary goal identification of fossil leaves, not classification of an extant group. Both found that phenetic analysis of their character sets generally associated different leaves of the same species but led to the recognition of no higher taxa. Their character sets tend to emphasize aspects of size and shape, most of which I found to be relatively invariable at the species level within the Phyllanthoideae, but highly variable within genera and higher taxa (Levin, 1986). However, given an unknown leaf from a member of the Phyllanthoideae, the characters I used would probably associate it with the correct genus or higher taxon.

Two problems arise using these characters for the identification of fossil leaves. The first is the obvious one: How do we know whether a particular fossil leaf belongs to the Phyllanthoideae? As I discussed in another paper (Levin, 1985), characters that neither Dolph, nor Hill, nor I included in our character sets may help narrow the choice of higher taxa. An example of such a character is the type of marginal toothing that Hickey and Wolfe (1975) found to be quite characteristic of families and higher taxa. Dolph (1976) and Hill (1980) excluded tooth type from their character sets to avoid statistically weighting the analysis in favor of toothed leaves at the expense of entire-margined leaves. I did not include tooth type in my study because it is invariable within the Phyllanthoideae; for the same reason I did not include other characters, e.g., pinnate versus palmate venation, that may help separate the leaves of the Phyllanthoideae from those of other taxa. Thus the placement of leaves in higher taxa requires not phenetic analysis using equally weighted characters, but the recognition of diagnostic characters that delimit large groups. Hill (1980) noted the same problem. Clearly, detailed examination of many more ex-

tant groups, coupled with cladistic analysis to identify diagnostic characters in those groups like the Phyllanthoideae that have relatively nondescript leaves, will be necessary before we can accurately relate many fossil leaves to leaves of their extant relatives.

The way SIMGRA analysis handled *Martretia* offers some indication of the way in which phenetic analysis might treat taxa not initially assigned to the correct higher taxon. Because of its substantial differences from other members of the Phyllanthoideae (although more in the combination of character states than in any particular character), *Martretia* joined late in the analysis. However, it still connected earlier than such aberrant but bona fide Phyllanthoideae as *Amanoa, Didymocistus, Discocarpus, Leptonema,* and *Spondianthus.*

The second problem, which was extensively addressed by both Dolph (1976) and Hill (1980), involves missing data. Many fossil floras include leaves that lack well-preserved higher order venation and/or cuticle. That the SIMGRA analysis of architectural characters alone yielded clusters that were less well resolved but substantially similar to clusters that formed using the entire character set suggests that cuticle may not always be essential to proper identification. However, as the preservation of venation becomes poorer, the confidence of identification could be expected to decrease considerably.

CONCLUSIONS

Phenetic analysis using leaf architectural and cuticular characters in the Phyllanthoideae produces groups similar to those in classifications based on characters more widely recognized as being of systematic value, such as floral morphology, palynology, and wood anatomy. Most exceptions appear not to be cases in which the leaf evidence is spurious, but in which there is also evidence from some other fields that the classifications are invalid. A similar but less well resolved clustering results from analysis of architectural characters alone. That numerical analysis yields such clear results in a group not known for having diagnostic leaves argues against the widely held idea that angiosperm leaves are so evolutionary and environmentally plastic that they are of little systematic value. At least in the Phyllanthoideae, the amount of parallelism and convergence in leaf architectural and cuticular characters is small enough that overall similarity

usually reflects presumed evolutionary relationship.

In a few cases, for example *Meineckia, Celianella,* some sections of *Cleistanthus,* and the phyllanthoid-branching genera in the Flueggeinae, excessive convergence does cloud relationship. In these cases, I feel that it is not so much a fault of the characters as it is the inherent weakness of systematic methods based on total similarity. The results of cladistic analysis of the same data even more closely resemble previous classifications (Levin, in press). The greater ability of cladistic methods to discriminate between divergent and non-divergent evolutionary change, and to factor out autapomorphies, minimizes the effects of these problems.

Because this is the first report of numerical analysis of the foliar morphology of a related group of flowering plants, the need for more studies remains. The characters employed were derived from systems developed for the description of fossil and modern angiosperms (Stace, 1965; Hickey, 1973) and are therefore widely applicable. Further examination and analysis of extant angiosperms should help us to understand better the patterns of leaf evolution in the flowering plants and to classify more confidently the leaves of fossil plants.

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